# Semiochemicals from a predaceous stink bug, *Podisus maculiventris* (Hemiptera: Pentatomidae)<sup>1</sup>

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#### **ABSTRACT**

A total of 19 volatile compounds from 6 different exocrine glands have been identified for the spined soldier bug, *Podisus maculiventris*. In addition to the exocrine glands responsible for the well-known stench of stink bugs, there are other odor-producing glands in adults and immatures whose secretions are not released in defensive contexts. The secretion from the large dorsal abdominal glands of adult males is a blend of (E)-2-hexenal, benzyl alcohol, and monoterpenes and serves as a long-range attractant pheromone. At least 4 parasitic species use this pheromone as a kairomone to find the bugs. The secretions from the other exocrine glands found in the spined soldier bug are also idiosyncractic, suggesting they, too, are pheromones. Possible pheromonal roles for the various volatile secretions of *P. maculiventris* are discussed.

Insects are fantastic natural product chemists. For example, Blum<sup>1</sup> listed 620 different defensive compounds (allomones) from about 1000 arthropod species, the majority insects. Intraspecific chemical signals (pheromones), often consisting of blends of compounds, have been identified and synthesized for nearly 250 insect species.<sup>2</sup> The so-called true bugs (order Hemiptera, suborder Heteroptera) account for about a tenth of the known insect allomones, but none of the synthetic insect pheromones.<sup>1, 2</sup>

Descriptions of sexually dimorphic exocrine glands in predaceous stink bugs (Pentatomidae: Asopinae)<sup>3</sup> suggest that these hemipteran insects also use pheromones.

Aldrich et al. 4 identified the components of a male-specific secretion from a common North American predaceous pentatomid, Podisus maculiventris (Say), the spined soldier bug. We have demonstrated that this secretion is, in fact, a long-range attractant pheromone and that insect parasites of P. maculiventris use the pheromone as a kairomone to locate this host.<sup>5</sup> The adult and immature stages of the spined soldier bug possess additional exocrine glands that produce the familiar stench of stink bugs,<sup>6</sup> plus other smaller exocrine glands of unknown function. Volatiles from six different exocrine glands have now been identified. In this paper, the positions and relative sizes of these glands are illustrated, the chemical compositions of the newly identified secretions are reported, and the compositions of previously examined secretions are updated by inclusion of recently identified compounds.

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## Methods and Materials

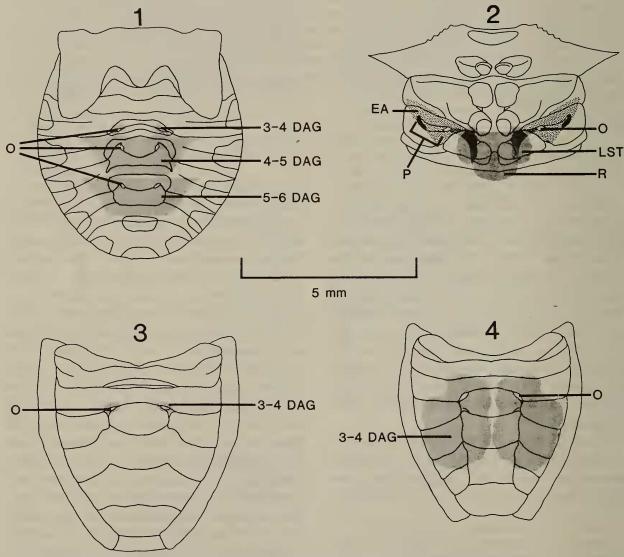
A culture of *P. maculiventris* was maintained in the laboratory on *Tenebrio molitor* L. (Rainbow Mealworms, Compton, CA) larvae and pupae. <sup>4</sup> Laboratory-reared bugs were used for all the drawings and chemical analyses.

Figures 1-4, illustrating the dorsal abdominal glands (DAGs) of adults and fifth-stage nymphs and of the metathoracic gland (MTG) of adult spined soldier bugs, were made using a Wild dissecting microscope equipped with a camera lucida.

Details of the preparation of exocrine

gland extracts have been previously reported. He is Briefly, exocrine glands were dissected from CO<sub>2</sub>-anesthetized bugs submerged in tap water, tissues surrounding the excised glands were removed, and the glands were macerated in  $50-200 \mu l$  of  $CH_2Cl_2$  or  $CS_2$ .

Gas chromatography (GC) of exocrine gland secretions, reported here for the first time (all the nymphal DAG secretions) or re-examined here (MTG and male 3-4 DAGs), was performed on a 14-m-fused-silica capillary column coated with a 0.25- $\mu$ m film of DB-1<sup>TM</sup> phase (J & W Scientific, Rancho Cordova, CA) using helium as the



Figs. 1-4. The exocrine glands of *Podisus maculiventris*. Finely stippled areas outline underlying glands, and numbers indicate the position of intersegmental openings. (1) Dorsal abdomen of a fifth-stage nymph. (2) Ventral thorax of an adult showing its metathoracic gland. (3) Dorsal abdomen of an adult female. (4) Dorsal abdomen of an adult male. DAG = dorsal abdominal gland; EA = evaporative area; LSTs = lateral secretory tubules; O = ostiole; P = peritreme; R = reservoir.

carrier gas (linear flow = 40 cm/sec). A Varian 3700 GC equipped with a flame-ionization detector was used with a Shimadzu C-R1B peak area integrator.

Gas chromatographic-mass spectrometric (GC-MS) analyses were conducted using a Finnigan 4500 GC-MS with 30-m columns coated with a 0.25- or 0.1-μm film of DB-1 phase. The GC oven temperature was usually held at 45°C for 2 min and then raised to 255°C at 10°/min. Minor modifications of this temperature program were made for some analyses to improve separations. Electron impact mass spectra were collected at 70 eV with the separator at 240°C and the source at 150°C.

Each compound was identified by comparision of its mass spectrum with the published mass spectrum and/or the mass spectrum of the authentic standard. 7, 8 Subsequently, all compounds identified by mass spectral data were cross-checked by comparison of the GC retention of the natural product to that of an authentic standard. Standards of previously identified P. maculiventris exocrine components were obtained commercially or synthesized as reported earlier.4 Tetradecanal was purchased from Aldrich Chemical Company (Milwaukee, WI), and trans-piperitol was purchased from PCR Research Chemicals, Inc. (Gainesville, FL). Piperitone (K & K Laboratories, Inc., Plainview, NY) was reduced with lithium aluminum hydride in ether to give a mixture of cis-piperitol (29%) and trans-piperitol (66%), plus several minor components by GC.

## Results

Morphology

Podisus maculiventris nymphs have orange DAGs opening between tergites 3 and 4, 4 and 5, and 5 and 6 (Fig. 1). The 3-4 DAGs are paired and spherical with gland cells surrounding a small cuticle-lined reservoir. Each gland opens exteriorly by a

single intersegmental ostiole. The 4-5 and 5-6 DAGs are large, unpaired dorso-ventrally flattened sacs that open exteriorly by a pair of ostioles. The 4-5 and 5-6 DAGs have large cuticle-lined reservoirs with glandular cells confined to their lower walls. 10 All the DAGs have muscularly controlled valves at their ostioles, and the 4-5 and 5-6 DAGs have stretch muscles inserted on the gland sacs, presumably to aid in ejecting the secretions. 10 Apparently, scent emission from DAGs can be independently controlled by these bugs. The contents of the 4-5 and 5-6 DAGs can be forcibly sprayed away from a nymph's body, and the valve-apparatus enables a nymph to aim the spray without moving its body. 10

At metamorphosis nymphal 4-5 and 5-6 DAGs are inactivated, and only deflated cuticular linings of these glands can be found in adults. The 3-4 DAGs are retained; in adult female bugs, the 3-4 DAGs appear to be identical to those of nymphs (Fig. 3), but in males the 3-4 DAGs are tremendously hypertrophied (Fig. 4). Metathoracic glands (MTGs), which are totally absent in nymphs, are present in both sexes of adults (Fig. 2).

The 3-4 DAGs of male and female adults are paired, orange, and have muscularly controlled ostioles as in nymphs. Although the adult male 3-4 DAGs are larger than the nymphal 4-5 and 5-6 DAGs, they do not have muscles attached to their walls. There is a pronounced sexual dimorphism of the tergal sutures associated with the 3-4-DAG ostioles in adults (Figs. 3 and 4). In females, a suture projects posteriorly from each ostiole connecting the 3-4 and 4–5 intersegmental sutures; the 5–6 and 6–7 intersegmental sutures are not connected by longitudinal stutures (Fig. 3). In males, the longitudinal suture from each ostiole extends posteriorly to the 6-7 intersegmental suture, and tergite 6 is bisected laterally by transverse sutures (Fig. 4). The sutures probably channel secretion laterally from the ostioles. 14 The more extensive system of sutures in males is probably an adaptation to disperse the larger volume of secretion from these 3-4 DAGs.

The MTGs of spined soldier bugs are not sexually dimorphic, but they are morphologically more complex than the DAGs (Fig. 2). The MTG is situated ventrally in the thorax, opening lateroventrally between the meso- and metathoracic coxae. There is a ridge around each ostiole (the peritreme) and a surrounding area of convoluted cuticle (the evaporative area) (Fig. 2, P and EA). The gland consists of two conspicuous parts; an unpaired, orange median reservoir, and a pair of white lateral secretory tubules (Fig. 2, R and LSTs). The lateral secretory tubules are multiply branched tubes formed by gland cells. Each mass of tubules empties into the reservoir through a duct near the ostiole. (Note that in Fig. 2 only the outline of each mass of LSTs is indicated.) The reservoir is lined by cuticle. Its wall contains a variety of evenly distributed secretory cells, and a ribbon-like accessory gland is embedded in the ventral wall. 10 The external MTG ostioles have

muscularly controlled valves, but no muscles are attached to the reservoir wall or lateral secretory tubules. The secretion is often exuded onto the evaporative areas when the bugs are disturbed; however, a spray of secretion can be ejected, as well. Apparently pentatomid bugs can aim a spray from the MTG only by adjusting their body positions.<sup>10</sup>

# Chemistry

Nymph 3-4 DAGs—These glands are minute and contain relatively little secretion. Of the 4 compounds identified (Table I) in an extract of five pairs of glands from fifth-stage nymphs, (E)-2-hexenal was the predominant component. The composition of this secretion is similar to that of adult females.

Nymph 4-5 and 5-6 DAGs—The secretions of these glands from a single fifth-stage nymph can be analyzed by GC.

Table I.—Chemistry of *Podisus maculiventris* exocrine gland secretions<sup>1,2</sup>

Compound	Nymph		Adult		
	3-4 DAGs	4–5 and 5–6 DAGs	male 3-4 DAGs	female 3–4 DAGs	MTG
(E)-2-hexenal	72.22	- 1	45.07	69.33	0.54
(E)-2-octenal	10.62			1.24	
(E)-2-decenal					_ 10.74
nonanal				0.59	
tetradecanal		1.01			
benzaldehyde	4.69			5.14	
(E)-4-keto-2-hexenal		25.73			12.79
(E)-2-hexenoic acid				23.70	
(E)-2-decenyl acetate					3.42
linalool		28.94	0.83		0.28
$(+)$ - $\alpha$ -terpineol			45.10		
terpinen-4-ol			0.93		
trans-piperitol			1.59		
cis-piperitol			0.07		
benzyl alcohol			6.41		
1-tridecanol					0.02
n-dodecane		0.73			1.54
n-tridecane	12.47	43.58			70.52
n-pentadecane					0.15

<sup>&</sup>lt;sup>1</sup>DAGs = dorsal abdominal glands, numbers indicate position of intersegmental openings; MTG = metathoracic gland.

<sup>&</sup>lt;sup>2</sup> Numbers listed in the table are % abundance of a component as determined by peak area from gas chromatograms (nymphal 4-5 and 5-6 DAGs, MTG, and adult male 3-4 DAGs) or reconstructed ion chromatograms (nymphal and adult female 3-4 DAGs).

Comparisons of extracts from the 4-5 and 5-6 DAGs of several individuals showed no consistent differences; therefore, the components identified in these secretions are listed together in Table I. The outstanding feature of these secretions is the presence of the monoterpene alcohol, linalool, as a major component. Tridecane and (E)-4-keto-2-hexenal are also major components, but (E)-2-hexenal was not detected in these secretions. Tetradecanal is a unique minor component.

Male 3-4 DAGs—Analyses of this glandular secretion have been previously reported<sup>4, 5</sup> and the secretion has been shown to constitute the long-range attractant pheromone of P. maculiventris. 5 However, we here revise our earlier report in that the compound tentatively identified as cispiperitol<sup>4</sup> is actually trans-piperitol (1.59%, Table I). A compound that coelutes with (+)- $\alpha$ -terpineol using packed GC columns can be separated by capillary column GC and has been identified as cis-piperitol (0.07%, Table I). The proportions reported here of previously known components differ somewhat from our earlier reports which used less accurate quantitation methods.

Female 3-4 DAGs—(E)-2-Hexenal is the predominant component in the secretion from these glands (Table I). (E)-2-Octenal and benzaldehyde were minor components, as in nymphs. Nonanal and (E)-2-hexenoic acid occurred in the female 3-4-DAG secretion, but not in that of nymphs.

Adult MTG—The compositions of male and female MTG secretions have been examined earlier and the secretions were not noticeably different.<sup>6</sup> The per cent abundance for the components of the MTG secretion listed in Table I were determined from a single P. maculiventris male of unknown age. (E)-2-Decenyl acetate is evidently produced only in the lateral secretory tubules,  $^{\circ}$  and (E)-2-decenal is probably enzymatically derived from the ester inside the median reservoir. 11, 12 The organic secretion in the reservoir is surrounded by an immiscible fluid that is apparently aqueous since it dissolved in the water of the dissecting dish when the reservoir wall was severed. The esterase and dehydrogenase enzymes are thought to be secreted by the accessory gland into the aqueous fluid. 11, 12 Tridecane and the other hydrocarbons are probably secreted by cells in the reservoir wall, 10 but the site of linalool synthesis is unknown. The organic secretion is a mixture of a polar phase and a non-polar phase. 13 The ratio of ester to corresponding aldehyde, as well as the ratio of these compounds to hydrocarbons and possibly linalool, can vary drastically with the age of the bug and the time since the secretion was last emitted. The occurrences of linalool and (E)-2-hexenal in this MTG secretion are noteworthy: this is the third exocrine gland secretion of P. maculiventris found to contain linalool, here as a minor component, and (E)-2-hexenal, which is a major component of all the 3-4-DAG secretions, is present but only as a very minor component.

## Discussion

Hemipterans emit chemicals to defend themselves against the attacks of predators and parasitoids. In the spined soldier bug, however, some exocrine secretions are not released in defensive contexts and are compositionally idiosyncratic. Since some, possibly all, of the *P. maculiventris* exocrine blends act as pheromones, this discussion will emphasize the possible pheromonal roles for these secretions and their kairomonal effects.

The chemical vocabulary of *P. maculiventris* is much greater than the list of 19 identified compounds might suggest. Many "minor" components remain to be identified, and surface waxes have yet to be analyzed chemically. Only the fifth-stage nymphs of *P. maculiventris* have been studied in detail; the exocrines of earlier stages may differ. The turnover rates of the various exocrine components are unknown, and, of the optically active components that have been identified, the enantiomeric composition has been determined only for

 $\alpha$ -terpineol. Even so, it is clear that *P. maculiventris* nymphs produce at least two unique blends; adults, at least three unique blends. What information might these exudates convey between individuals of the species, and how have other organisms, particularly parasitoids, usurped these signals?

The male 3-4-DAG secretion attracts both sexes of adults, and nymphs are at least moderately attracted to the pheromone. Attracted adult bugs fly to the odor source, and males release this secretion during courtship (JRA, personal observation), so the secretion apparently functions as a long-range attractant pheromone and as a short-range mating stimulant. The natural pheromone contains (+)- $\alpha$ -terpineol, but an artificial pheromone, made with racemic  $\alpha$ -terpineol, is as attractive to the bugs as one made with (+)- $\alpha$ -terpineol. Single pheromone components were unattractive to P. maculiventris in the field. 17 Whether individual pheromone constituents, including cis- and trans-piperitol, will elicit particular behaviors has not yet been studied. We believe that wild P. maculiventris males, which are usually smaller and mature faster than females, 18 may first search for food and then attract a mate with their 3-4-DAG secretion.

At least four parasitic species sabotage this long-range pheromone system. Females of two flies, Hemyda aurata Robineau-Desvoidy and Euclytia flava (Townsend) (Diptera: Tachinidae), go the pheromone and lay eggs on the spined soldier bugs they see in the area, 5 sometimes even on other pentatomid species confined near P. maculiventris synthetic pheromone (unpubl. data). The male flies are attracted to the vicinity of calling P. maculiventris males and appear to defend a territory in order to mate with incoming female flies. Female Telenomus n. sp. (Hymenoptera: Scelionidae) are attracted to the male 3-4-DAG secretion and become phoretic on mated female bugs. 5,19 Eventually female wasps oviposit in recently laid P. maculiventris eggs. 19 Females of a fourth parasitic species, an ectoparasitic biting midge, Forcipomyia crinita Saunders (Diptera: Ceratopogonidae), also find spined soldier bugs by orienting to the male 3-4-DAG secretion. The (-)- $\alpha$ -terpineol in pheromone made with racemic  $\alpha$ -terpineol inhibits the response of *E. flava* and *F. crinita* to the pheromone, but *P. maculiventris* and *T.* n. sp. are unaffected by the presence of (-)- $\alpha$ -terpineol.

Neither live female *P. maculiventris*<sup>5</sup> nor synthetic material blended to mimic the female 3-4-DAG secretion attracted bugs or parasitoids. Thus, this exocrine secretion probably acts only over a short distance. Male bugs may recognize a female and/or assess her willingness to mate by the odor of her 3-4-DAG secretion. Parasitoids, especially the *Telenomus* species, might sense near-by female bugs or recognize females they encounter by the smell of their DAG secretions.

Pheromonal roles for the MTG secretion of *P. maculiventris* are, at this point, conjectural. The MTG scent of an irritated *P. maculiventris* adult arouses close-by conspecifics, as in some other hemipteran species; <sup>10</sup> therefore, in this context the secretion seems to function as an alarm pheromone. Since neither the MTG nor its secretion are sexually dimorphic in *P. maculiventris*, a sexual role for this secretion is questionable. The composition of the MTG secretion can vary with age, <sup>11</sup> and this could be important information for courting bugs.

In our airborne trapping experiments, when an adult pentatomid dies, the contents of its MTG rapidly escape from its reservoir. Some scavenging flies (e.g. milichiids) are attracted to hemipteran MTG secretions (Dr. Paula Mitchell, Louisiana State University, personal communication) or to esters similar to those in MTG secretions. This may explain how these scavengers quickly locate dead or injured adult bugs.

First-stage P. maculiventris nymphs and many terrestrial hemipterans are highly gregarious, with later stage nymphs becoming progressively more solitary with each molt. Ishiwatari 22, 23 identified (E)-2-hexenal in whole body extracts of cabbage bug

nymphs, Eurydema rugosa (Pentatomidae), and showed that at low concentrations this compound promoted aggregation of nymphs whereas high concentrations of (E)-2-hexenal dispersed aggregated nymphs. Perhaps in P. maculiventris, the 3-4-DAG secretion is the short-range pheromone responsible for aggregating young nymphs, and emission of the 4-5- and 5-6-DAG secretions disperses these aggregations. One species of predaceous pentatomid is known whose nymphs hunt singly but recongregate to molt.<sup>21</sup> If P. maculiventris nymphs that become dispersed while searching for prey periodically reaggregate, a longerrange aggregation pheromone might have evolved. The occurrence of linalool as a major constituent of the large DAG secretions in P. maculiventris may have evolved as part of such a pheromonal message because nymphal DAG secretions usually contain only unbranched compounds. 10

Tachinid parasitoids may use linalool to locate spined soldier bug nymphs. In preliminary experiments, performed before the nymphal DAG secretions had been analyzed, we field-tested some components of the male 3-4-DAG and the MTG secretions, singly and in mixtures. Four H. aurata flies were caught in traps baited with 5  $\mu$ l of linalool and 5  $\mu$ l of (E)-2-hexenal. Hemyda aurata and E. flava do sometimes parasitize nymphs in the field.<sup>24</sup> These tachinids may respond to the odor of a provoked nymph or to the odor of DAG components evaporating from the cast skin since the exocrine gland contents are shed at each molt. If tachinid parasitoids were able to home in on the DAG odor from exuviae, this would ensure that eggs are laid on newly molted nymphs and have ample time to hatch before the next molt of the host.

In summary, P. maculiventris has an elaborate pheromone system that has been exploited by at least four parasitic insect species. The male-produced attractant pheromone has been most intensively studied; the behavioral correlates for the other exocrine secretions are, at this point, speculative. Future testing of synthetic P. maculi-

ventris exocrine blends should answer many remaining questions. Spined soldier bugs are probably not exceptional among Hemiptera in using pheromones—this insect order is a veritable treasure-trove for pheromone researchers.

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